Abiotic Stresses and Endophyte Effects

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Abstract

Abiotic stresses consist of nonorganismal, nonpathogenic factors that inhibit plant function. Tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh.] is widely symbiotic with a naturally occurring endophytic fungus [*Neotyphodium coenophialum* (Morgan-Jones and Gams) Glenn, Bacon, and Hanlin], which confers many benefits to its host that favor its ecological fitness for growth, persistence, and reproduction. Tolerance or resistance to water deficit (drought) and soil chemical stresses, such as low pH and low mineral availabilities, comprise the two principal categories of abiotic stresses. Enhanced tolerances of tall fescue to such stresses due to endophyte symbiosis are not universally expressed, and the mechanisms by which the symbiosis imparts such benefits are not well understood. Plant responses to endophytes involve a complex of physiological, biochemical, and morphologic adjustments that are conditioned by host genotype, endophyte genotype, environment, and their interactions. Endophyte strains that lack ergot-alkaloid production capability have been discovered recently, culminating the 30-yr search for ways to combat the deleterious effects of wild endophytes in *Lolium* species. When some of these novel endophytes are transferred into elite tall fescue germplasm, host plant persistence and vigor are enhanced. These innovations will allow grassland managers to exploit the agronomic benefits, while avoiding the detrimental aspects of the tall fescue–endophyte symbiosis, for profitable livestock production.

For much of the past 30 years, tall fescue research has focused on the detrimental effects of toxins produced by a naturally symbiotic endophyte (*Neotyphodium coenophialum*) on livestock performance and metabolism (see Chapter 1, Hoveland, 2009, this publication). Early efforts to mitigate the toxic effects of endophyte infected (E+) tall fescue included eradicating the endophyte from seedstocks and eliminating existing E+ stands and reseeding with endophyte free (E–) tall fescue. It seemed that in many pasture and turf plantings, E+ plants persisted better than E– plants where drought stress and insect predation occurred. At the same time, scientists in New Zealand observed that perennial ryegrass (*L. perenne* L.) infected with a similar endophyte (*N. lolii* Latch, M.J. Christensen & Samuels) showed superior resistance to Argentine stem weevil [*Listronotus bonariensis* (Kuschel)]. Evidence suggested that host plants had competitive and adaptive advantages

when infected with endophytes. This had tremendous implications for management and cultivar development for pastures and turf and, on a basic level, for understanding the ecology of plant communities (i.e., plant autecology).

A number of plant physiological and ecological processes are influenced by host–endophyte symbiosis; however, a simple, unifying mechanism by which the endophyte promotes host fitness is not apparent. In general, *Neotyphodium* endophytes confer resistances to biotic stresses (i.e., herbivory by insects and mammals, including grazing livestock) and abiotic stresses (e.g., drought and soil deficiencies) and possibly even promote growth. Biotic and abiotic stresses can interact to influence host–endophyte responses. For example, when the presence of toxic alkaloids deters grazing and allows plants to thrive with high leaf area and tiller density, the plants can acquire resources (i.e., water and nutrients) and persist in stressful conditions. The complex relationship between the host plant and endophyte is a function of direct and indirect effects of the endophyte on metabolic and developmental processes influencing plant production and persistence (Malinowski and Belesky, 2000; Malinowski et al., 2005a). We review the attributes of host plant–endophyte interactions with emphasis on tall fescue responses to abiotic stresses associated with drought and soil mineral deficiencies. The reader is referred to in-depth reviews of water relations (Frank et al., 1996) and mineral nutrition (Mayland and Wilkinson, 1996) of cool-season grasses to complement this chapter.

Zone of Adaptation and Relation to Endophyte

Tall fescue is the primary cool-season perennial forage grass adapted to the east-central and mid-southern United States (see Chapter 3, Hannaway et al., 2009, this publication). Abiotic stresses in this zone include mineral nutrient deficiencies and drought and high temperature stresses during summer. Nutrient imbalances occur because upland soils, in much of the range in which tall fescue is adapted, tend to be highly weathered and eroded. Field trials showed that E+ stands yielded more and persisted longer than E– stands in the southern portion of the adaptation zone, including Texas (Read and Camp, 1986), Louisiana (Joost and Coombs, 1988), Arkansas (West et al., 1993), and Georgia (Bouton et al., 1993).

Endophyte helps tall fescue persist south of the dashed line shown on the tall fescue adaptation zone map (Fig. 4–1). The line represents a transition, from north to south, of increasing summer water deficit caused by high evaporative demand and low soil water-holding capacity. For example, erodible, rocky soils predominate in the Ozark Highlands of southern Missouri and northern Arkansas, where summer temperatures are high. Similar soil limitations occur in the southern Appalachian Mountains and adjoining regions; however, summer temperatures, and thus evaporation rates, are lower at the higher elevations in the Appalachians than in the Ozarks.

Local zones of stress-prone soils occur north of the dashed line, where endophyte aids persistence, and deep, loamy soils occur south of the line, where E– tall fescue can persist. Endophyte and associated antiherbivory characteristics of infected plants help tall fescue compete and survive when growing where conditions favor the growth of other plant species.
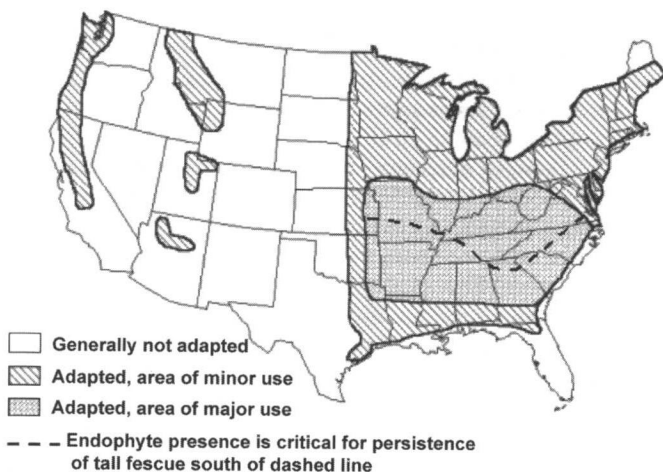
Fig. 4–1. Zone of adaptation and use of tall fescue in the United States (West, 1998).

Water Deficit Stress

Tall fescue pastures in Texas dominated by E+ plants (94% infestation) had greater persistence than low-endophyte (12% infestation) pastures (Read and Camp, 1986). Greenhouse and small-plot field experiments showed that E+ plants had enhanced drought tolerance (Arachevaleta et al., 1989; West et al., 1993). The mechanisms enabling this tolerance are complex and probably involve numerous factors. Protecting growing points (apical meristems) from irreversible desiccation is one way to ameliorate the impact of drought. Osmotic adjustment, that is, promotion of active solute accumulation in cell sap, was greater in the base of vegetative tillers, where cell growth occurs, of E+ than of E− plants, with the magnitude of adjustment related to tiller survival (Elmi and West, 1995). Cell solute accumulation slowed the loss of cell turgor in or near growing points, protecting tissue capable of regenerating after drought. More simple sugars accumulated in leaf sheaths of drought-stressed E+ than E− plants; this could help minimize desiccation or freezing damage to cells (Richardson et al., 1992). In a field trial, water content of the outer leaf sheath of vegetative tillers was greater in E+ than E− plants, suggesting that water loss would be less and the plant would be protected from wilting (Elbersen and West, 1996). Shoot mass and tiller numbers often are greater in E+ than in E− plants (Arachevaleta et al., 1989; De Battista et al., 1990; Hill et al., 1990; West et al., 1993), but some tall fescue genotypes are unaffected or grow less when endophyte infected (Belesky et al., 1989). A greater rate of tillering by certain E+ plants delays tiller number decline (West et al., 1993).

An indirect means by which endophyte enhances host drought tolerance is by deterring herbivory. The production of certain chemical constituents, including a wide array of alkaloids, could cause grazing animals to avoid endophyte infected tall fescue (see Chapter 13, Bush and Fannin, 2009, this publication). Plants could then retain leaves, tillers, and roots and be better able to survive stressful conditions. Grazing reduces the amount of leaf area available for photosynthesis,

reducing the ability of the plant to regrow and sustain energy reserves in tiller bases and crown tissue. Overgrazing can lead to energy depletion, weaken the root systems, and diminish the ability to acquire water, especially when precipitation is limited. Drought stress appears to enhance production of ergot alkaloids in E+ tall fescue (Arechavaleta et al., 1992), thereby amplifying the endophyte protection effect. Likewise, deterrence of root-feeding organisms by E+ plants can enhance water acquisition by the host. When endophyte was removed from tall fescue, a large increase in root-knot nematode (*Meloidogyne marylandi* Jepson & Golden) occurred on roots, reducing root mass and lowering osmotic adjustment in the tiller growth zone (Elmi et al., 2000).

Proposed mechanisms of endophyte-enhanced host plant persistence include a range of cellular metabolism and whole-plant responses (Fig. 4–2). Stomata of E+ plants appeared to close earlier at the onset of drought compared with E– plants grown under highly controlled conditions (Belesky et al., 1987; Elmi and West, 1995). In contrast, field-grown E+ plants tended to have greater stomatal conductance and less leaf rolling, a symptom of water deficit stress, than E– plants of the same genotype (Elbersen and West, 1996). This might reflect the ability of E+ plants to develop large root systems that improve access to soil water, delaying onset of drought stress symptoms. Various abiotic stresses, including drought, heat, cold, nutrient deficiency, and high solar radiation, can incite excess production of reactive oxygen species, or free radicals, which can damage cell organelles and membranes and impair normal plant function. Endophytes appear to enhance production of the antioxidants superoxide dismutase (Fike et al., 2001; West et al., 2005) and total phenolics (Malinowski et al., 1998a). Endophytes occurring in the leaf sheaths and meristematic zone of vegetative tillers during summer water-deficit events may thus produce signals at the hypha–plant cell wall interface that translate into plant cytoplasmic biochemical responses responsible for cell turgor maintenance and free-radical quenching. The endophyte effects on host fitness are not always positive. Host and endophyte genotypes and environment,

Physiological Responses of Endophyte Infected Plants

Light and Temperature
- R:FR Ratio Influences Alkaloid Production
- Temperature Response Unknown
- Possible Cold Tolerance as a Function of Polyol Accumulation
- Photosynthesis and Stomatal Function

Water Deficiency
- PolyHydroxy Alcohol
- Carbohydrates
- Loline Alkaloids
- Indole Acetic Acid
- Abscisic Acid
- Stress Proteins
- Stomatal Regulation

Mineral Toxicants
- Hydrogen Ion
- Aluminum Ion
- Divalent Ion Exclusion

Mineral Deficiency
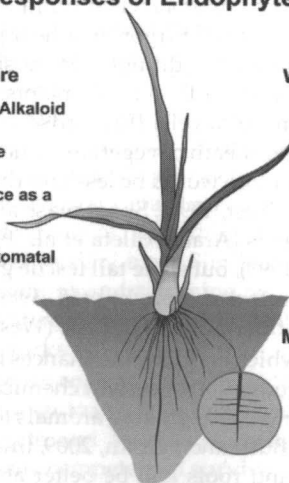- Phosphorus
- Calcium
- Magnesium

Fig. 4–2. Some physiological responses of endophyte infected tall fescue plants.

including management, interact in often unpredictable ways to modulate phenotypic expression, such that endophyte symbiosis can be neutral or even detrimental to the host (West, 2007).

The creation of novel host–endophyte associations that were devoid of ergot alkaloids was a significant technological advance to help mitigate the occurrence of fescue toxicosis in grazing livestock (Bouton and Easton, 2005; Nihsen et al., 2004). Bouton et al. (2002) demonstrated superior stand survival of 'Jesup' tall fescue inoculated with endophyte AR542, a novel endophyte that does not produce ergot alkaloids compared with tall fescue infected by wild, toxic endophyte. Lamb weight gains when grazing the novel host–endophyte plants were similar to those achieved when grazing E– pastures. Novel, nontoxic endophytes now provide a means to understand and benefit from *Neotyphodium* endophytes as mechanisms of improving host persistence (see Chapter 20, Bouton, 2009, this publication).

Another recent advance in tall fescue technology has been the development of cultivars from Mediterranean germplasm that exhibit partial summer dormancy as a means of improving summer drought survival (Norton et al., 2006). Traditional tall fescue cultivars used in temperate climates are considered "summer-active"—growth continues in summer as long as soil moisture is plentiful. Cultivars such as Kentucky 31 (KY-31) apparently need the *Neotyphodium* symbiosis to persist during drought. Endophyte infection did not influence growth and survival of summer-dormant fescue populations in northwest Arkansas (Underwood et al., 2008). In fact, summer-dormant types showed virtually complete stand survival after drought, irrespective of endophyte infection status. Endophyte infection did benefit summer-dormant tall fescue in the semiarid environment of north-central Texas (Malinowski et al., 2005c). These authors concluded that summer-dormant types show potential for survival in the subhumid to semiarid transition zone of the southern Great Plains of Oklahoma and Texas, where summer-active types do not persist.

Light-Related Factors

The amount and type of light reaching a plant canopy influences the ability of a plant to acquire water and nutrients, allocate dry matter, and carry on energy-dependent metabolic processes. In contrast with our current knowledge of the influence of endophyte and water-related stress on the host, there is little information on the effect of endophyte infection and the response of the host plant to light quantity and quality. Belesky and Malinowski (1999) considered how light affects host–endophyte responses to abiotic stress. Light influences allocation of photosynthate among plant structures and regulates the expression of tillers. Since E+ plants appear to have greater rates of tillering, interacting effects of light quality and endophyte infection could influence this process and ultimately the plant's competitive ability in a range of canopy environments.

Uncut canopies of Jesup tall fescue infected with a native endophyte produced more pyrrolizidine alkaloids in full sun than in plants grown in shaded (either ~35 or 80% of full sunlight) conditions (Belesky, unpublished data, 2005). Shade increased the pyrrolizidine alkaloid concentration when the same host–endophyte association was clipped to either a 5- or a 10-cm residue. When Jesup was infected with AR542, pyrrolizidine alkaloid concentrations were less that those occurring in the Jesup–native endophyte association, but did increase in

concentration with decreasing light, irrespective of how the canopy was managed. Jesup devoid of endophyte was devoid of pyrrolizidine alkaloid. Ergot alkaloids were present in Jesup infected by the native endophyte, but were absent from Jesup devoid of endophyte or host to AR542. Shading decreased the concentration of ergot alkaloid when canopies were not cut, but had minimal effect when cut to a 5- or 10-cm residue (Belesky, unpublished data, 2005). The antioxidants represented by total phenols decreased in leaf blades as light availability decreased, and Jesup host to a native endophyte produced greater concentrations of phenols than did either Jesup devoid of endophyte or Jesup host to AR542 (Belesky, unpublished data, 2005). These observations provide important clues for managing silvopasture or home lawns where trees are common features of the landscape. Endophyte infected plants provide a beneficial mechanism of natural herbivore control by eliciting alkaloid production. Shading seems to increase alkaloid production as well, so that home site landscaping that includes both trees and turf might have complementary influences on plant persistence by deterring insects that consume turf plant species.

Herbage production or plant size is linked to competitiveness of plants (Harper, 1977). Dense swards influence light quality by absorbing more of certain light wavelengths within the canopy. The altered light environment leads to different amounts and quality of light, which can influence tiller production, leaf elongation, and phytomass. Changes in allocation affect the amount of photosynthate available for growth, storage, or use in secondary metabolite production, as well as nutrient and water acquisition. High temperatures and high light intensities are likely to occur simultaneously, especially in southern portions of the tall fescue adaptation zone (Fig. 4–1). Ability to tolerate water deficit and maintain photosynthetic capability at high leaf temperature and light intensity is a competitive advantage for cool-temperate origin species in the southeastern United States. This ability contributes to the versatility of tall fescue as a forage resource and provides pasture managers with plant material of a high quality for use in areas dominated by warm-season species.

Soil Conditions

Tall fescue persists under a wide range of soil conditions, including those of high exchangeable Al, low pH, low P availability, and where distinct physical challenges associated with shallow and eroded soils occur (see Chapter 3, Hannaway et al., 2009, this publication). Apparently, tall fescue can avoid or tolerate chemical and physical stresses by making physiological and morphological adaptations that in some instances seem to be associated with the presence of endophyte. For example, plant-available P supply often is limited in acidic soils. Endophyte, although localized in the aboveground portion of the plant, elicits some of the same responses in tall fescue as mycorrhizal fungi do in other plant species, particularly improved P and water acquisition by the host (Wittenmayer and Merbach, 2005). Grasses commonly form symbiotic associations with mycorrhizal fungi, but *Neotyphodium* spp. endophytes appear to suppress mycorrhizal colonization in tall fescue (Baker, 1987; Chu-Chou et al., 1992; Guo et al., 1992), perennial ryegrass (Müller, 2003), and annual ryegrass (*L. multiflorum* Lam.) (Omacini et al., 2005), suggesting alternative strategies to ensure survival under suboptimal soil conditions.

Cheplick et al. (1989) suggested that the host plant incurred a metabolic cost to support the endophyte. The cost, expressed in terms of smaller plants, would not be realized unless stressful environmental conditions occurred, with differences between E+ and E− associations greater in young than in well-established plants. Responses varied among cultivars and clones within cultivars in later experiments on mineral stress (Belesky and Fedders, 1995; Zaurov et al., 2001). Endophyte infected plants either grew better, similar to, or were impaired relative to E− plants when nutrients were limited. Growth of very young E+ plants was depressed relative to E− plants at low nutrient status, and no differences in growth were apparent under high nutrient conditions. Early seedling development and resource allocation in host plants of similar genotype but with different endophyte strains suggest that early seedling growth, up to 6 wk of age, and tiller production of certain E+ plants is slower than those in E− plants when grown with an ample nutrient supply (Belesky et al., 2008).

Nitrogen

The influence of endophyte on host N metabolism was among the early discoveries related to mineral nutrition of host–endophyte associations. Lyons et al. (1990) showed that concentrations of tissue N were less in E+ than in E− plant leaves, regardless of N supply. This led to work suggesting a more efficient conversion of N to growth in E+ plants (Arechavaleta et al., 1989). Several experiments have shown that N fertilization enhanced alkaloid production in E+ tall fescue and thus could lead to plants more harmful to livestock than plants growing in N-poor soils (Arechavaleta et al., 1992; West et al., 1994). Nutrient deficiency, specifically N deficiency, seemed to restrict growth of some E+ plants of *Lolium* and taxonomically related species (Cheplick et al., 1989) and poverty grass [*Danthonia spicata* (L.) P. Beauv. ex Roem. & Schult.], a species common on marginal and low fertility sites (McCormick et al., 2001). Recently, Pecetti et al. (2007) observed that N fertilization seemed to benefit the persistence of E+ plants, but that the extent of benefit depended on an interaction of local growing conditions with origin of host–endophyte association. When N was supplied, the stand declined regardless of host–endophyte association or location. Stand decline was related to increased competition from co-occurring warm-season grass species, indicating the complex interaction of host–endophyte associations and management on plant community structure.

Soil Acidity

Nutrient Availability

Tall fescue is grown on millions of hectares in the warmer portions of the humid eastern United States. It is used on soils where low pH and limited nutrient supply restrict plant productivity, caused by interactions among prior land use practices, relatively high rainfall amounts, and soil geochemistry. Plants that are adapted to acidic soils possess a variety of mechanisms that enable them to tolerate or overcome adverse soil chemical conditions. For example, soil acidity affects plant growth through a complex of chemical changes in the rhizosphere involving increased H^+, Al^{3+}, and Mn^{2+}. These include inhibition of metal cation (Ca^{2+}, Mg^{2+}) uptake, a decrease in P and Mo solubility and increased efflux of nutrients and metabolites from roots. Root morphology and function also change when soil chemical conditions are less than ideal for plant growth. For example,

when soil water is scarce, some species can explore large areas of soil, and, in other instances, mineral challenges can elicit or suppress the production of fine root structure (Huang, 2001). The net effect modifies nutrient activity in the root zone, expressed as physiological and morphological adaptations to stress in root tissue.

Fescue–Endophyte Interactions

Host–endophyte responses to management and environment can vary in unpredictable ways that complicate our understanding of responses to abiotic stresses. Endophyte infected tall fescue produced less root mass than E– plants under simulated acid rain, although the response depended on plant age (Cheplick, 1993). Soil acidity influenced dry matter production and allocation differently in clones of five tall fescue–endophyte associations (Belesky and Fedders, 1995). In general, E+ plants tended to tolerate soil acidity, but not all associations did so to the same extent, attesting to the role of genetic interactions between host and endophyte.

Genotype Effects

Fine-leafed fescues (e.g., *Festuca rubra* L., *F. ovina* L., *F. longifolia* Thuill.) tolerate low to intermediate soil fertility. When grown under Al-induced stress, E+ fine-leafed fescues had longer and heavier roots and heavier shoots than E– lines (Liu et al., 1996), suggesting greater Al tolerance in E+ than in E– plants. Larger root systems could be a function of plant age, rooting volume, or an expression of fine-leafed fescue morphology. Response to Al-induced stress varied among specific clonal lines and associated endophytes of fine-leafed fescues (Zaurov et al., 2001), with growth influenced by plant genotype–endophyte interaction. In some cases, shoot mass was greater in E+ than in E– plants grown on soils with high exchangeable Al, but in most instances infection did not influence shoot mass. High Al levels suppressed growth of some E+ clones. Consequently, broad generalization about endophyte infection and tolerance to Al stress could not be made.

Effects of Roots

A major advance in understanding endophyte involvement in mineral nutrition was the discovery of apparent chemical modifications in the rhizosphere and the regulatory effects that nonspecific root exudates had on uptake of certain minerals (Malinowski et al., 1998a; Malinowski and Belesky, 1999a,b; Malinowski et al., 2000, 2005b). Release of phenolic-like compounds with the ability to reduce iron (Fe^{3+}) and chelate Al and Cu seemed to be associated with enhanced P acquisition by E+ tall fescue plants (Malinowski and Belesky, 2000). Roots of E+ (*N. lolii*) perennial ryegrass plants also released phenolic compounds (Zhou et al., 2003), but not much is known about involvement of these exudates in mineral uptake (Malinowski et al., 2005b).

Tolerance by Plants

Mechanisms of soil acidity tolerance in grasses are complex, particularly in E+ grasses. Low soil pH and high soluble Al concentrations are associated with restricted root growth and inhibit N uptake and N supply to growing leaves. Phenolic-like compounds can chelate Al and may help plants transport Al in nontoxic forms. Tall fescue accumulated much less Al in shoots than roots, suggesting a means to sequester Al in the roots (Foy and Murray, 1998). Phenolic-like

compounds exuded from roots of E+ tall fescue appeared to be involved in Al tolerance. Aluminum was excluded from E+ plants in hydroponic conditions (Malinowski and Belesky, 1999a). More Al (47%) and P (49%) were desorbed from root surfaces of E+ than E− plants, depending on root dry matter. More Al (35%) but less P (10%) was found in root tissues of E+ plants, suggesting that Al is sequestered in roots and P translocated to shoots. Changes in nutrient solution pH occurred for hydroponically grown E+ tall fescue, especially under limited P and high Al (Malinowski and Belesky, 1999a; Malinowski et al., 1999). In control (nonfertilized) soil and soil supplied with a low amount (13 mg P kg^{-1}) of commercial P fertilizer, soil pH increased more rapidly when associated with E+ than with E− plants (Malinowski and Belesky, 1999a).

Phosphorus

Tall fescue often grows where pH and factors related to soil acidity diminish P availability and plant growth. Agronomic practices and growing conditions influence P availability and are important when managing E+ tall fescue. For example, P uptake and herbage production were greater in E+ than in E− plants when soil P availability was low; however, mass was less in E+ than in E− plants at high soil P availability (Malinowski et al., 1998b). Low P led to greater specific root length (i.e., finer roots) in E+ plants and greater concentrations of P, Mg, and Ca in roots and shoots of E+ than E− plants (Malinowski et al., 2000). Infected plants had more root dry weight (10%) and greater relative growth rate (16%) than E− plants when P was supplied as phosphate rock, but endophyte mediated responses were minimal when conventional P fertilizer was applied (Malinowski and Belesky, 1999a). This trend was verified in a separate investigation of endophyte influence on mineral concentrations in tall fescue (Vazquez-de-Aldana et al., 1999). Endophytes accumulate P and apparently place some demand on P absorbed by the host (Azevedo and Welty, 1995).

Effect of Soil Type

Rahman and Saiga (2005) grew E+ and E− tall fescue clones selected from native populations cultivated on Black Andisol (low P content, high contents of other nutrients) and Red Andisol (high P content, low contents of other nutrients) soils under controlled conditions. When grown in Black Andisol soil, E+ plants had greater cumulative shoot dry weight and regrowth rates than E− plants, while in Red Andisol the opposite was the case. In P deficient Black Andisol, endophyte infection increased P, K, Ca, and Mg uptake and transport within plants. Although root exudates were not evaluated, results suggested that an internal signaling system between the endophyte and the grass host leads to faster adjustments to environmental factors, when compared to responses occurring in E− plants.

Effect of the Endophyte

Two endophyte related mechanisms for P uptake appear in tall fescue grown in P deficient conditions: (i) altered root morphology and (ii) increased activity of root exudates. Endophyte infected tall fescue grown in nutrient solution produced roots with smaller diameters and longer root hairs than E− plants, regardless of the amount of P available for plant uptake (Malinowski et al., 1998a). The authors also showed that E+ tall fescue produced greater amounts of phenolic-like compounds in roots and shoots when P was limited. Zhou et al. (2003) reported

similar findings for perennial ryegrass. These compounds could leak out of roots to change the availability of mineral nutrients or influence microbial or biological activity in the rhizosphere near the root surface. Since phenolic-like compounds were detected in E– plants as well, they might not be endophyte specific but regulated by endophyte when the host plant encounters additional stresses.

Garner et al. (1993) proposed that P was involved in ergot alkaloid biosynthesis for tall fescue endophytes, linking P nutrition with ergot alkaloid production in E+ grasses. Ergot alkaloid concentrations increased as P availability increased in endophyte–tall fescue associations, especially those with low ergot alkaloid production capability (Malinowski et al., 1998b).

Zinc

Endophyte infected perennial ryegrass was able to grow in the presence of excessive Zn (Monnet et al., 2001), possibly because of a mechanism that appears to exclude Zn from roots and which is similar to that proposed by Malinowski et al. (1998a) and Malinowski and Belesky (1999a). Endophyte infection seems to exclude Zn but allow Mn to accumulate in leaves. Zinc accumulates in some soils near industrial sites; E+ plants might serve as an effective cover crop to stabilize the Zn (see Chapter 28, Joost, 2009, this publication) and its effects on wildlife habitat in the soil (Stewart and Martin, 2003). Endophyte infected plants of perennial ryegrass appear to have greater tolerance of Zn than do E– plants (Monnet et al., 2001, 2005). The response was measured in terms of damage to photosystem II function. The E+ plants were able to maintain photosynthesis and growth at higher soil Zn levels than were E– plants.

Copper

Copper concentrations were less in E+ than in E– plants (Dennis et al., 1998), with deficiency expressed as decreased Cu-related immune function (Saker et al., 1998). Cattle grazing E+ tall fescue showed symptoms of deficiency (coat condition and hair color) by the end of the grazing season in Kansas (Coffey et al., 1992). Copper concentrations in KY-31 tall fescue grown in Virginia and Mississippi differed as a function of endophyte infection (Allen et al., 1997). Steers consuming E+ tall fescue grown in Virginia had lower serum Cu concentrations than steers fed E– plants, while no differences in serum Cu were observed for steers fed tall fescue grown in Mississippi. Apparently, Cu uptake is influenced by endophyte and soil composition (see Chapters 12 [Strickland et al., 2009] and 16 [Waller, 2009], this publication). Endophyte infected plants seem to restrict translocation of potentially toxic metal ions to aboveground tissues. However, low concentrations of essential micronutrients and bioavailability factors could raise concerns about nutritive quality in extensively managed tall fescue pasture.

Tall fescue typically harbors endophyte genotypes (strains) whose alkaloids elicit toxicoses in grazers; however, the presence of endophyte could confer adaptive benefits to the plant–endophyte association. Some endophytes do not cause toxicity or produce toxic alkaloids when removed from their natural host and grown in a different plant genotype. One such novel endophyte strain, AR542, when inserted into Jesup tall fescue increased Cu^{2+} binding activity by root exudates of tall fescue when grown in a P deficient nutrient solution. Under experimental conditions, the phenomenon did not appear to interfere with Cu accumulation in shoot tissues, but under field conditions, where Cu

concentrations in soil are much lower and P may easily limit growth, the novel endophyte may have reduced Cu availability to the plant (Malinowski et al., 2003). This process may interfere with Cu uptake under field conditions and diminish concentrations of minerals antagonistic to Cu, such as Mo, thereby reducing Cu absorption from forage by grazing animals.

Other Minerals

Information on the influence of endophyte on mineral composition of forage grasses is limited (see Chapter 11, Burns, 2009, this publication). Vazquez-de-Aldana et al. (1999) investigated the influence of endophyte infection on mineral composition of tall fescue. Nitrogen and Mg concentrations were greater in E+ than in E– tall fescue, and time and infection status interacted to influence concentrations of N, P, Ca, and Mg. Less Ca and more Mg accumulated in E+ than in E– plants, while P and K were not affected (Hoveland et al., 1983). Consistently higher concentrations of Fe occurred in E– than in E+ plants (Dennis et al., 1998). In some instances the influence was indirect and mediated by grazing livestock, with nutrients redistributed across the landscape in different spatial patterns depending on the endophyte status of the sward (Wilkinson et al., 1989).

Plant–Grazer–Soil Interactions

Endophyte infected tall fescue plants influence the grazing behavior of livestock and thus the redistribution of mineral nutrients in pasture associated with urine and dung pats (Wilkinson et al., 1989; Franzluebbers et al., 2000; Schomberg et al., 2000). Manure deposition is not a completely random process, since concentrations of nutrients occur at sites in the pasture where livestock congregate, rest, or seek shade or protection from wind and rain. Wilkinson et al. (1989) used soil K as an indicator of nutrient redistribution in response to grazing management and host–endophyte characteristics. Potassium concentrations were greatest near shade, water, and mineral-salt sources, probably as a consequence of deposition of livestock feces and urine at these sites. Soil associated with E+ tall fescue stands had greater concentrations of organic C and N than soils associated with E– tall fescue (Franzluebbers et al., 1999). This might be related to differences in soil respiration attributable to E+ plants that were somewhat less than respiration rates occurring in soils of E– tall fescue stands. The patterns of grazing behavior associated with E+ tall fescue have the potential for significant impact on nutrient management and biogeochemical processes in pastures. Detritivore populations differed in soils depending on host endophyte infection status (Omacini et al., 2007). The change in microfaunal population and resulting differences in litter decomposition would very likely have immediate and longer-term influences on nutrient availability in pastoral systems. Differences in soil organic matter concentrations would influence mineral nutrient availability and water-holding capacity, thereby influencing plant productivity and persistence.

Acknowledgments

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